The Animal Phylogeny

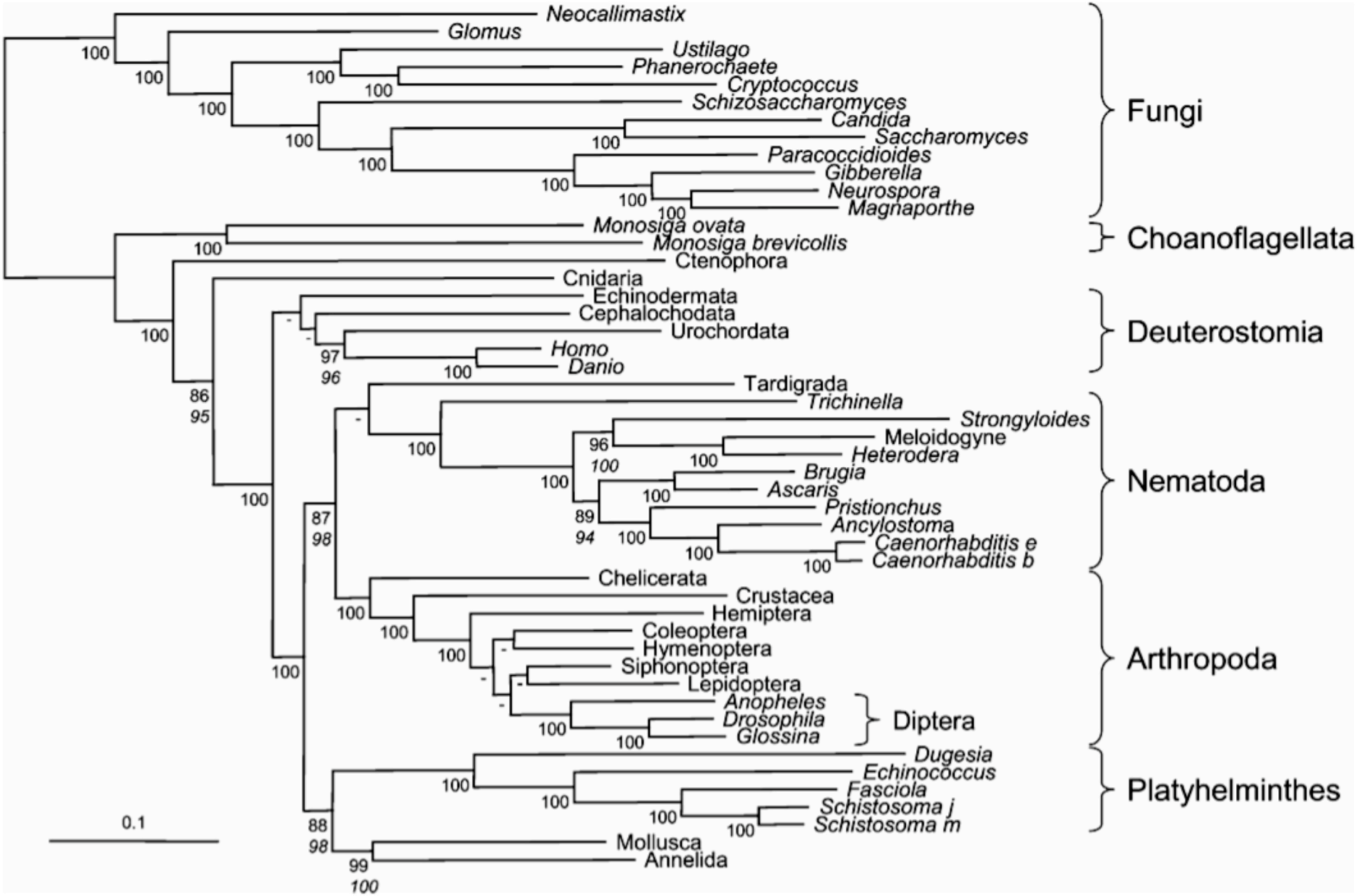
and the Fundamental Importance of Taxon Sampling

Hervé Philippe, Henner Brinkmann, Denis Baurain

February 20th 2006

The New Animal Phylogeny

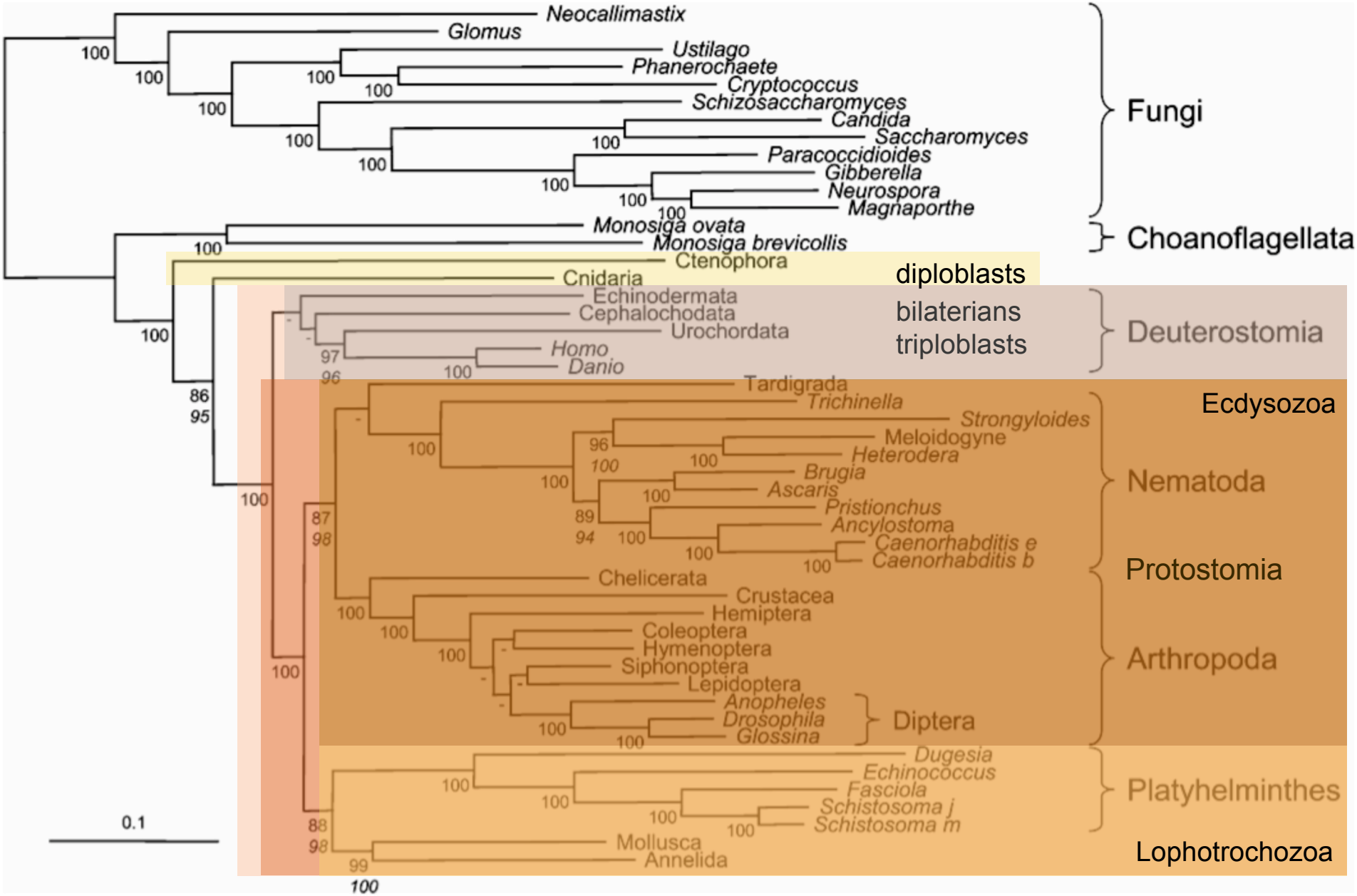
71 slow-evolving genes x 37 animal taxa (20,705 sites) ; ML tree



Philippe et al. (2005) Mol Biol Evol 22:1246-1253

The New Animal Phylogeny

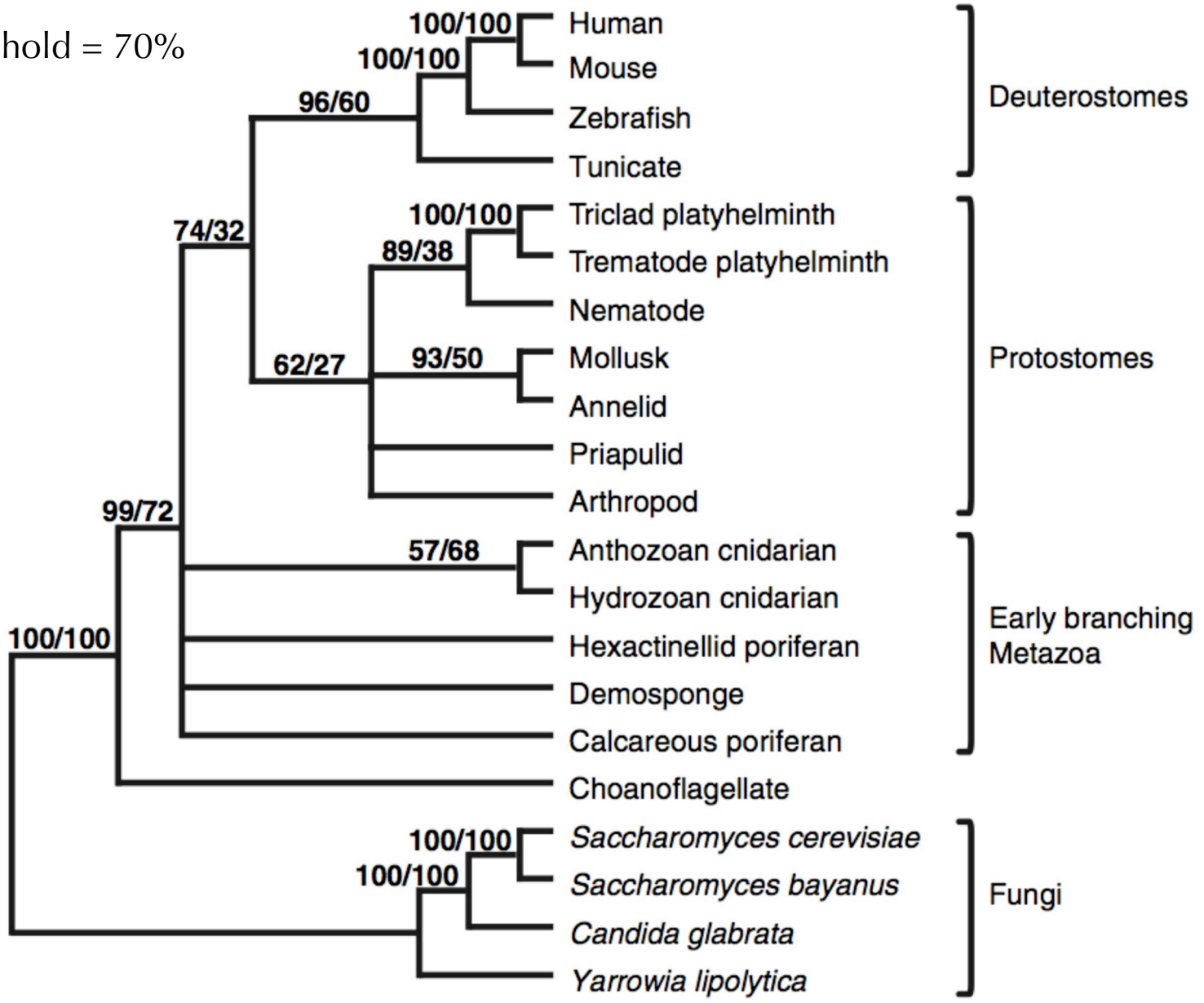
71 slow-evolving genes x 37 animal taxa (20,705 sites) ; ML tree



Philippe et al. (2005) Mol Biol Evol 22:1246-1253

Lack of resolution among most metazoan phyla

threshold = 70%

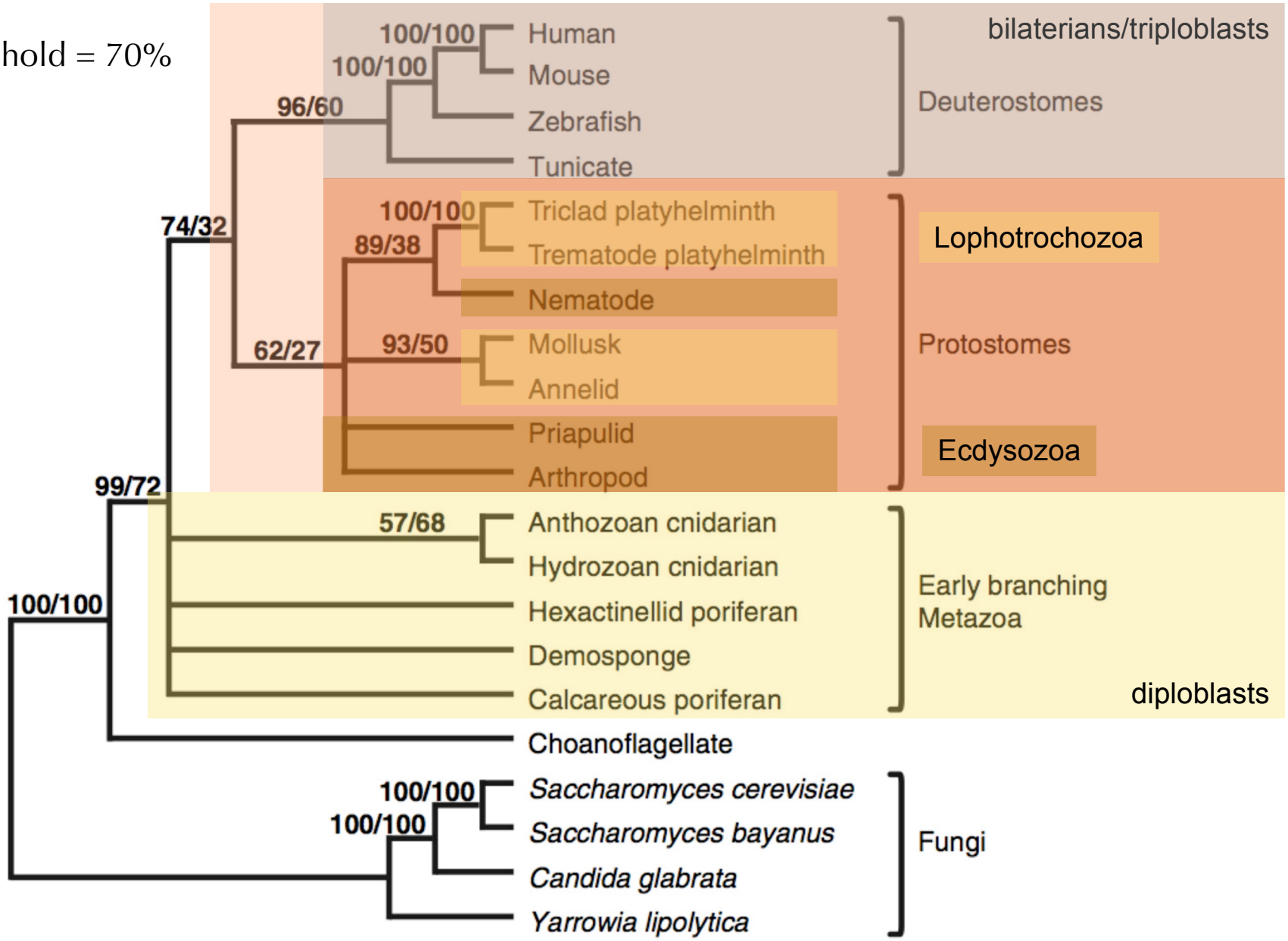


50 genes x 17 animal taxa (12,060 sites) ; ML/MP tree

Rokas et al. (2005) Science 310:1933-1938

Lack of resolution among most metazoan phyla

threshold = 70%



50 genes x 17 animal taxa (12,060 sites) ; ML/MP tree

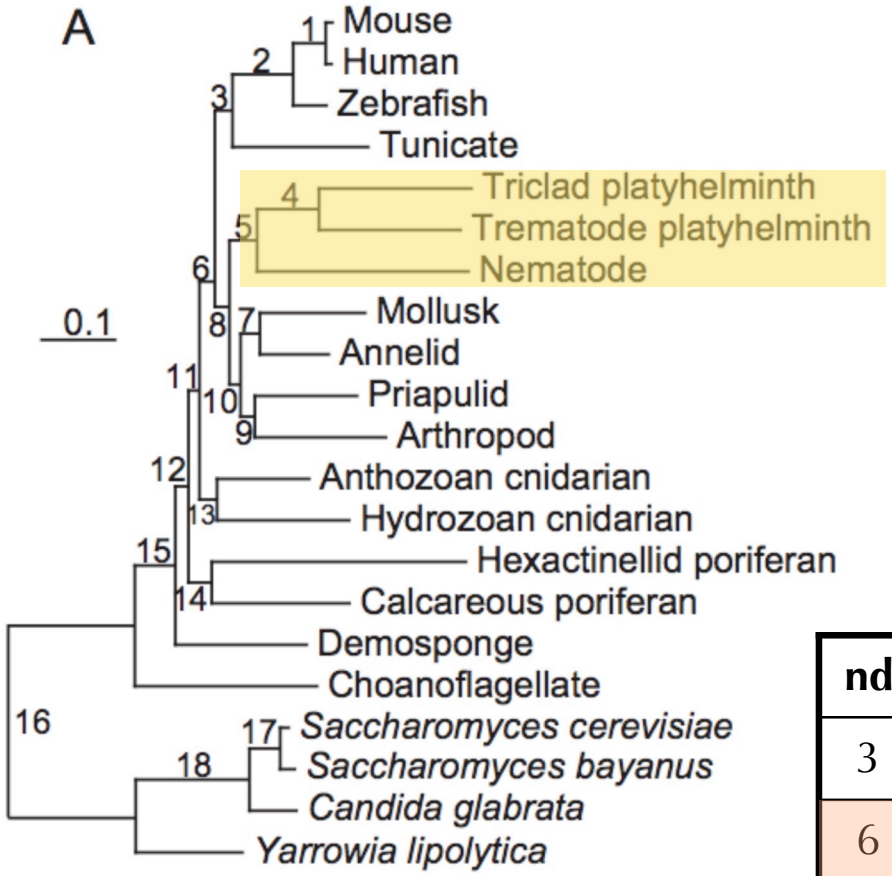
Rokas et al. (2005) Science 310:1933-1938

Possible causes for the lack of resolution

- **long branch attraction** artifacts
  - removal of nematods and platyhelminths
- presence of **rogue taxa**
  - computation of **leaf stability indices** (bootstrap-based)
  - removal of poriferans and cnidarians
- deviations in **amino-acid composition**
  - removal of 6 scattered taxa violating the **homogeneity assumption**
  - computation of a **LogDet** NJ tree

No subset of taxa seems to decrease the resolution.

Effect of the removal of 3 long-branched taxa



nd	clade	before	after
3	Chordata	96/60	94/66
6	Bilateria	74/32	100/72
7	mollusks + annelids	93/50	97/78
8	Protostomia	62/27	100/72
9	priapulids + arthropods	79/07	69/35
13	Cnidaria	57/68	55/63

ML tree ; BS from ML/MP trees

supplementary data of Rokas et al. (2005) Science 310:1933-1938

Investigating the apparent systemic lack of resolution

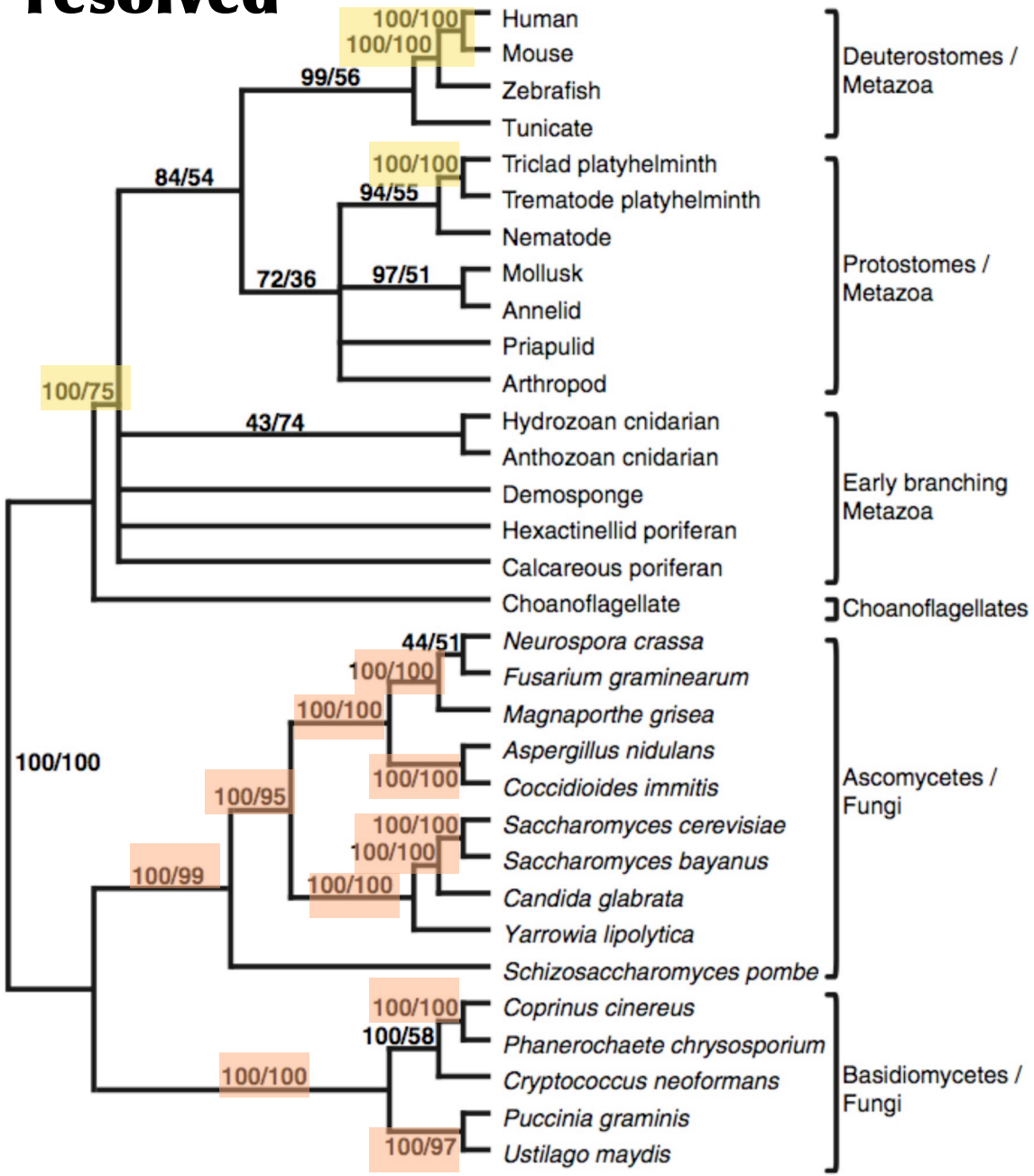
- amount of **missing data**
  - design target: 20%
  - removal of priapulid (68%) and mollusk (54%)
- total **amount of data** (12,060 sites)
  - 56% of sites are variable
  - 31% are parsimony-informative
- **distribution** of informative sites among topologies
  - **likelihood mapping** (no resolution for diploblasts)
  - **resampling** up to 100,000 sites (slightly better support)

Nothing seems to explain the lack of resolution.

The rationale for comparing Metazoa and Fungi

- aim is to **distinguish between 2 hypotheses**
  - **mutational saturation** has erased phylogenetic signal
  - lack of resolution as a signature of **closely spaced cladogenetic events** in early animal evolution
- **Why** Fungi?
  - **sistergroup** relationship (Opisthokonta)
  - approximately same **date of origin** (according to fossils and molecular clocks)
  - same **set of genes** available (49 out of 50)
  - roughly same **tempo** (ML-estimated distances) and same **mode** of evolution (AA substitution matrices)

Fungi are better resolved than Metazoa



50 genes x (17 + 15) taxa (12,060 sites) ; ML/MP tree

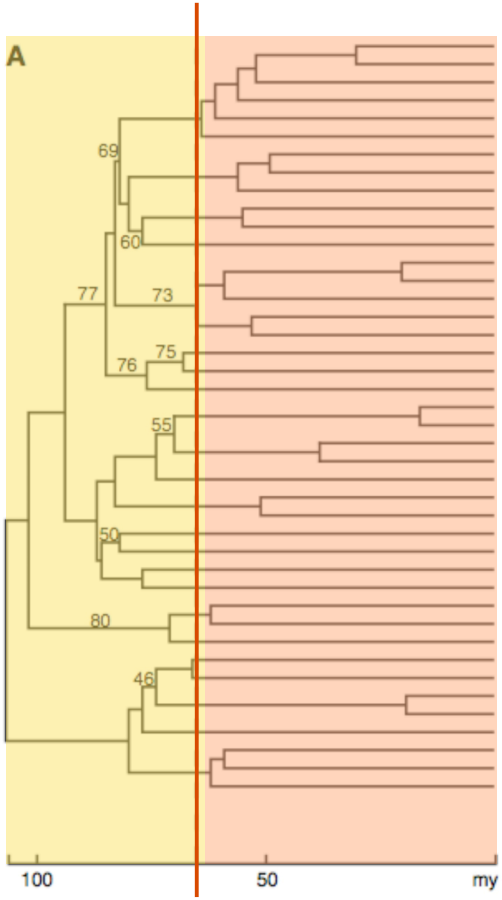
Rokas et al. (2005) Science 310:1933-1938

The case for a radiation compressed in time

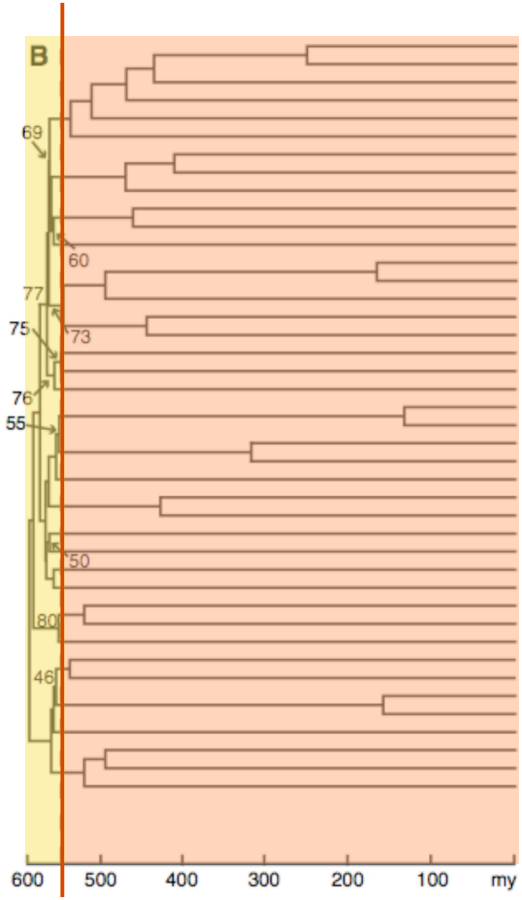
- **molecular** data
  - Fungi have a higher **stemminess** (F = 0.201) than Metazoa (F = 0.121)
  - Fungi have more **parsimony-informative** sites (5,015 vs 3,701) and less **singleton** sites (1,518 vs 3,080) than Metazoa
- **paleontological** data
  - poriferans, cnidarians and bilaterian fossils appear within a **50 MY time-frame**

Evidence for the so-called *Cambrian explosion*?

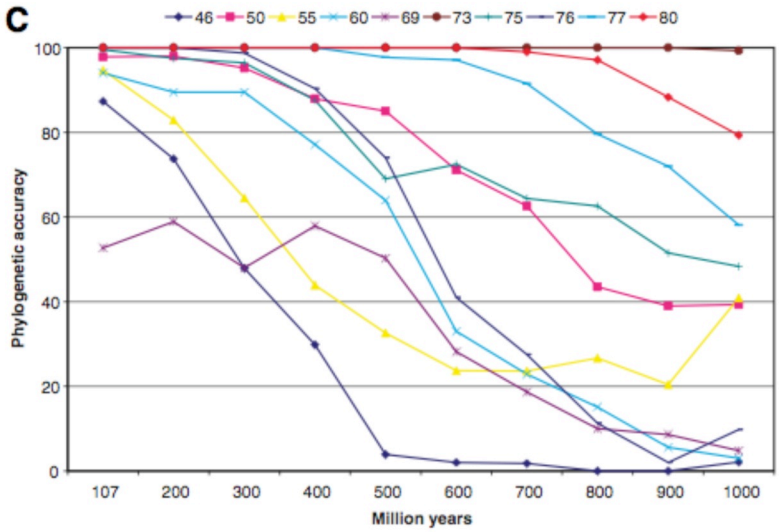
Simulation analysis of the mammalian radiation

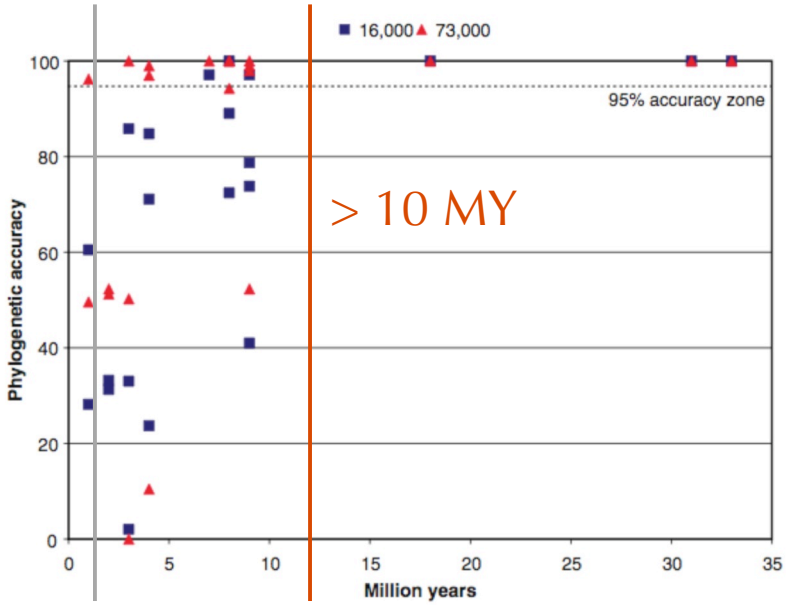


42 MY ; 107 MYA



42 MY ; 600 MYA





The lack of resolution of the animal tree is interpreted as the signature of a radiation compressed in time.

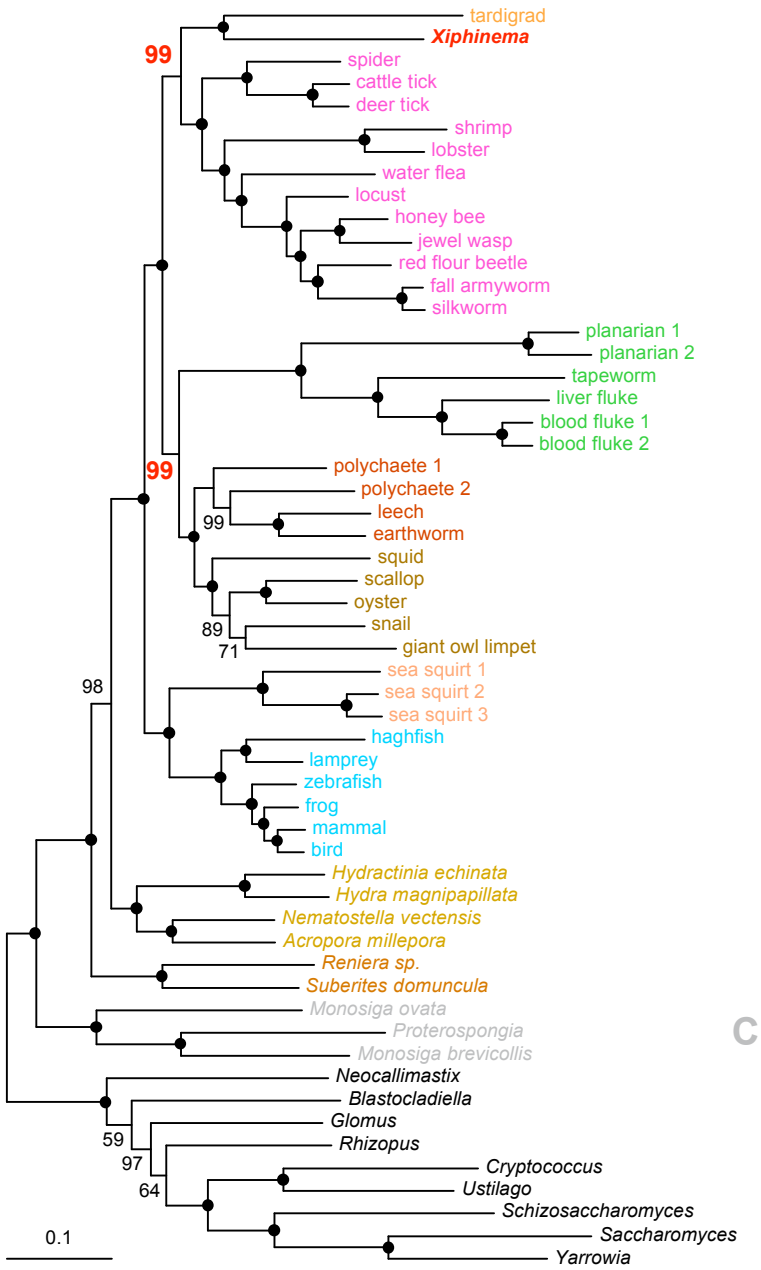
covarion model ; 16,000 sites ; MP (NJ)

Rokas et al. (2005) Science 310:1933-1938

Debunking Rokas et al. (2005)...

- Rokas et al. (2005) are likely wrong
  - very few taxa
  - extensive use of MP
  - ignorance of previous studies
  - dismissing of alternative explanatory hypotheses
  - misleading simulations
  - biased conclusions
- We will demonstrate that...
  - animal evolution can be resolved (**no explosion**)
  - **taxon sampling** is of fundamental importance

A tree with more genes and a denser taxon sampling



Arthropoda

Platy-helminthes

Annelida

Mollusca

Tunicata

Vertebrata

Cnidaria

Porifera

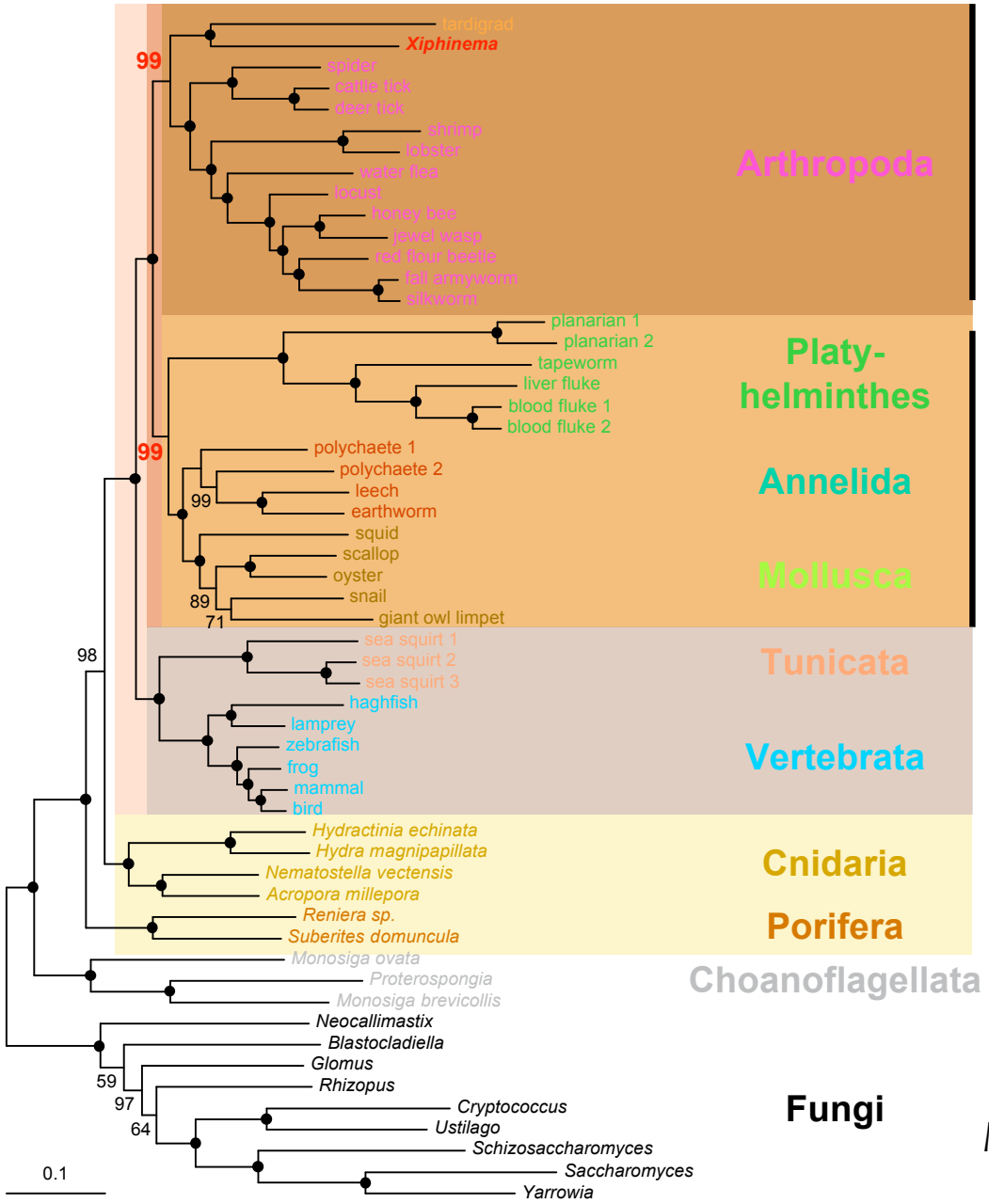
Choanoflagellata

Fungi

133 genes x 47 animal taxa (31,092 sites)
ML tree ; bullets = 100% bootstrap support

Philippe et al. (unpublished)

A tree with more genes and a denser taxon sampling



133 genes x 47 animal taxa (31,092 sites)
ML tree ; bullets = 100% bootstrap support

Philippe et al. (unpublished)

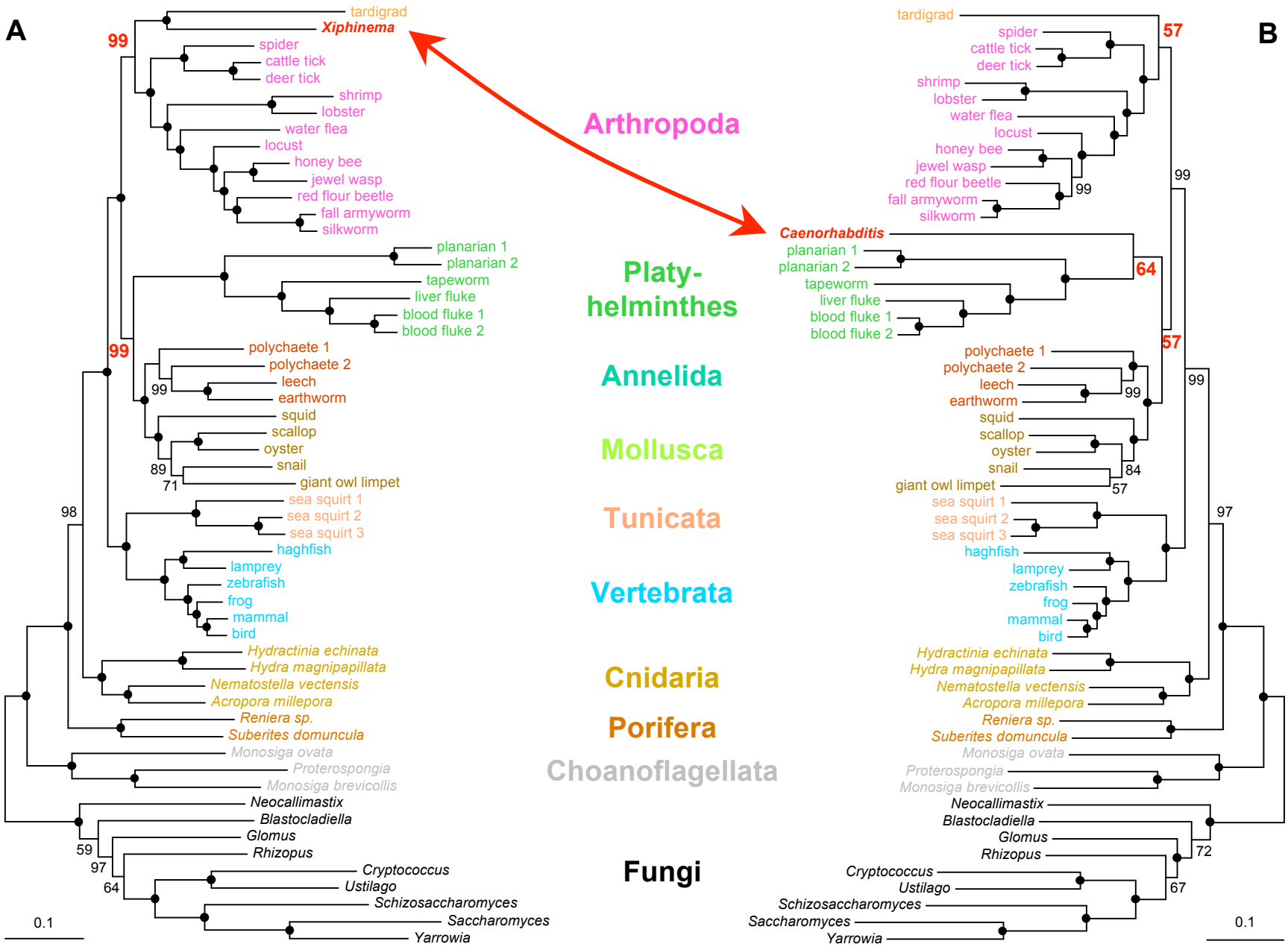
More genes or more/better taxa?

- Philippe et al. (unpublished) vs Rokas et al. (2005)
  - 133 (31,092 sites) vs 50 (12,060 sites)
  - among 10 random drawings of 50 genes, only one unresolved tree was retrieved
- Philippe et al. (2005)
  - 71 slow-evolving genes (20,705 sites) are able to resolve most internodes in the animal tree

A **large dataset is needed but not enough** to accurately resolve difficult phylogenetic relationships.

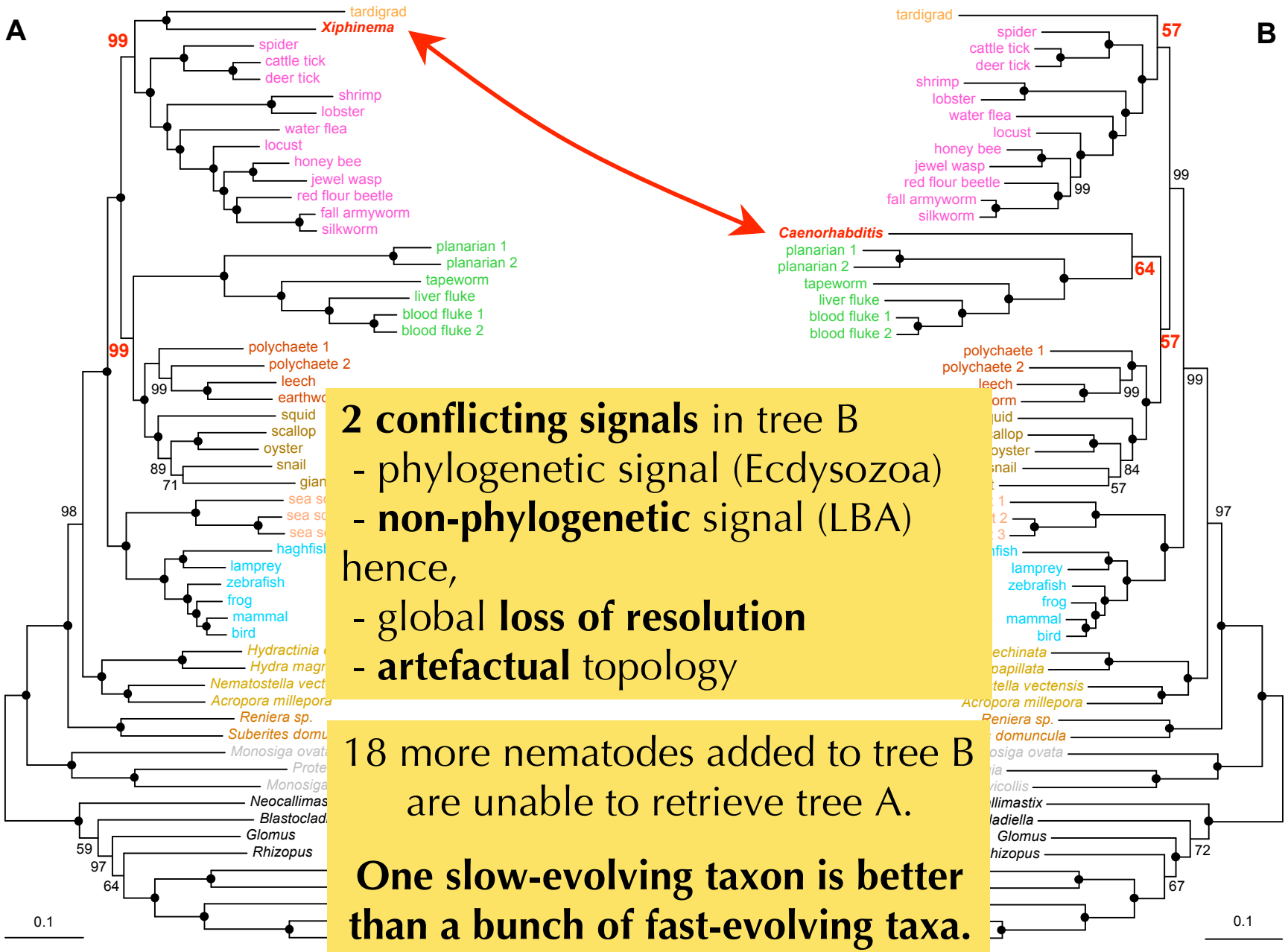
Let's show we also need **adequate taxon sampling**.

Taxon sampling and non-phylogenetic signal



Philippe et al. (unpublished)

Taxon sampling and non-phylogenetic signal



2 conflicting signals in tree B
- phylogenetic signal (Ecdysozoa)
- **non-phylogenetic** signal (LBA)

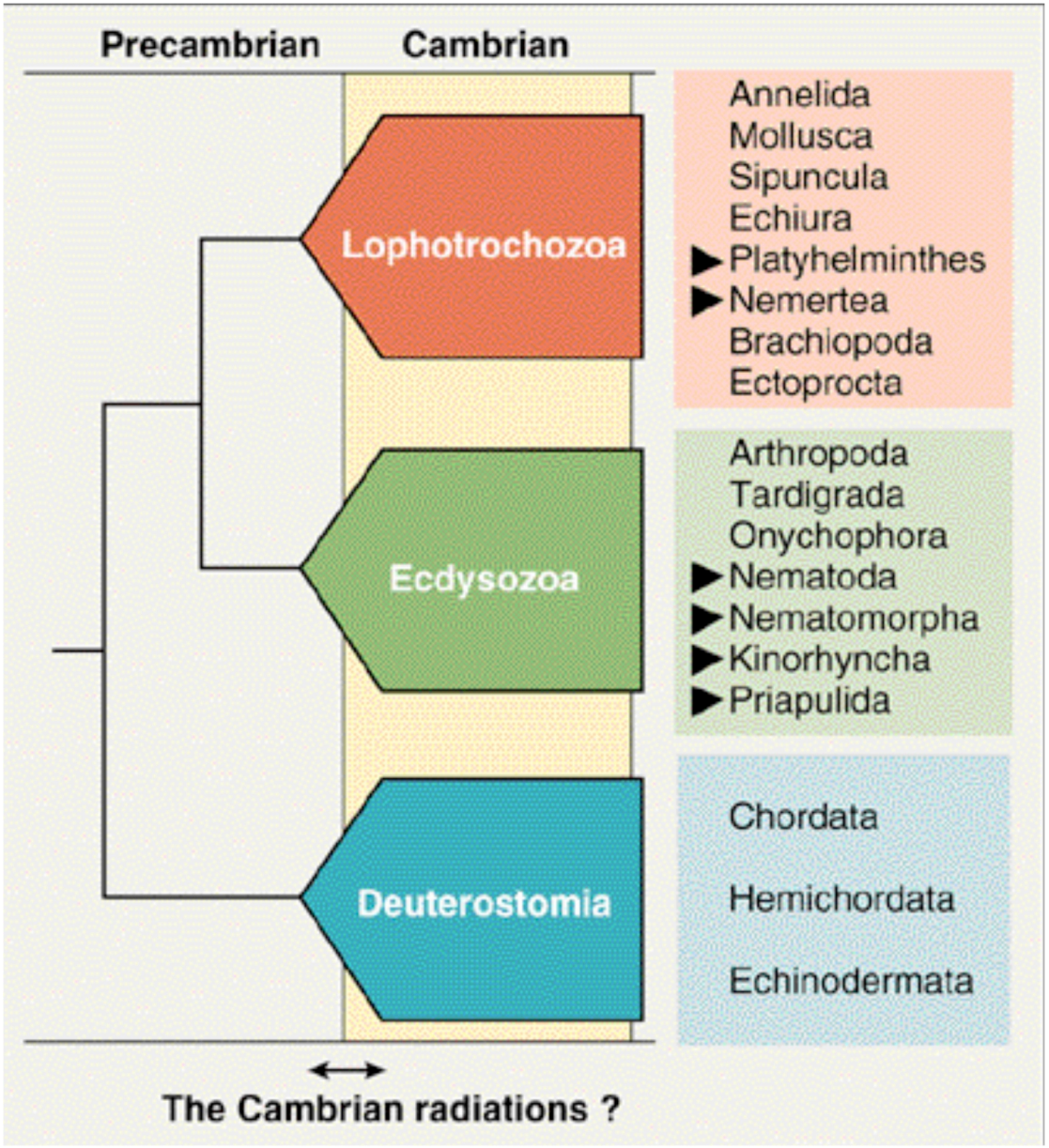
hence,
- global **loss of resolution**
- **artefactual** topology

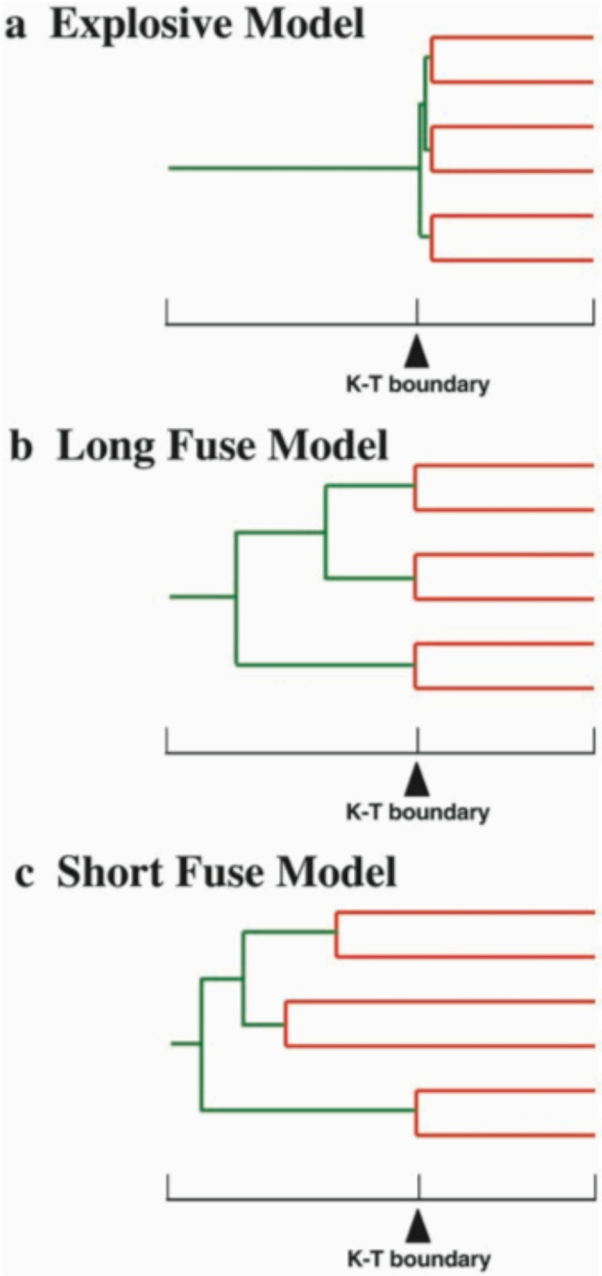
18 more nematodes added to tree B are unable to retrieve tree A.

One slow-evolving taxon is better than a bunch of fast-evolving taxa.

Philippe et al. (unpublished)

The Cambrian Explosion revisited





Balavoine et al. (1998) Science 280:397-398 ; Springer et al. (2003) PNAS 100:1056-1061